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# THE EFFECTS OF ACID AND ALKALINE SOLUTIONS UPON THE WATER RELATION AND THE METABOLISM OF PLANTS<sup>1</sup>

ALFRED DACHNOWSKI

The problem of the physiological water requirement of plants (4) is essentially only a phase of that greater problem,—the quantity of water retained by living organisms, by cells and tissues, under a variety of normal and pathological conditions, or during development and the evolution of succulency (of fruits etc.) in the higher plants. It is clearly evident that an attempt to answer this question should also be a step toward an analysis of the ways and means by which tissues and cells hold their normal or abnormal amount of water, *i. e.*, the forces which are active in the process of absorption and retention of water.

Investigators of late years have sought the explanation of the variations in the amount of water absorbed and retained by plants, as well as by animals, in differences in osmotic pressure, and more recently a theory has been proposed to account for it on the basis of the variable "affinity" of colloids for water. The pages that follow concern themselves with a consideration of a few experiments and with the inquiry whether the acceptance of the suggestion here advanced merely necessitates a revision of explanations or whether it adds another to the forces already considered as active in the water relation of plants.

A review in detail of the arguments which have been brought for and against the osmotic conception of water absorption by cells (8), or the one from the point of view of the state of colloids (7,17), seems out of place at this time, since these are questions which on the basis of the facts now available can not be decided as yet. Though probably overrated, the two theories have contributed the experimental data upon which depends much of the fundamental progress of the physico-chemical physiology of organisms.

The experiments detailed below have been made with the view toward establishing experimentally what importance, if any, hydrolytic reactions may have in determining the amount of water absorbed and retained by plants during germination and growth. That the

<sup>1</sup> Contribution from the Laboratory of Plant Physiology, Ohio State University.

velocity and the equilibrium point of hydrolysis may be altered by acids and alkalis is suggested by a number of facts (1), but the conception that such changes may control the course of metabolism and the physiological water requirement of plants needs to be placed on a firmer basis. Attention has been given both to a series of experiments with seeds and with cuttings of plants.

Dry seeds of *Phaseolus multiflorus* and *Zea mays* were used which had been in the laboratory for at least three years and proved to be of a low germinating power. The seeds were weighed and placed in glass-covered crystallizing dishes, each containing 100 cc. of solution. At various intervals, the seeds were removed from the solution, carefully dried with filter paper and weighed. The difference in weight, *i. e.*, in the amount of water retained, with the gain or loss on the part of each set of seeds was calculated also in percentage of the original weight of the dry seeds.<sup>2</sup> The data contained in tables I to VI indicate the

TABLE I

THE WATER CONTENT OF BEAN SEEDS (*Phaseolus multiflorus*) IN ACID SOLUTIONS  
Two seeds in each 100 c.c. solution

Time Interval in Hours		H <sub>2</sub> O	H <sub>2</sub> SO <sub>4</sub> n/800	HNO <sub>3</sub> n/800	HCl n/800	HCl n/3,200	HCl n/6,400
Hours	Minutes						
		2.090	1.995	2.055	2.580	2.240	2.580
2		2.692	2.400	2.080	2.835	2.261	2.720
6	30	3.508	2.862	2.120	3.510	2.519	3.120
16	30	4.220	3.758	2.901	4.305	3.960	4.211
20	30	4.220	4.025	3.312	4.545	4.320	4.549
26	30	4.341	4.330	4.018	5.180	4.912	5.160
40	30	4.463	4.501	4.320	5.452	5.258	5.495
48	30	4.397	4.472	4.370	5.478	5.280	5.500
65		4.430	4.497	4.384	5.510	5.260	5.615
89	30	4.365	4.580	4.403	5.520	5.220	5.630
116		4.250	4.440	4.409	5.540	5.155	5.600
137	30	4.230	4.400	4.445	5.465	4.970	5.535
164	30	4.223	4.203	4.468	5.410	4.840	5.360
195		4.220	4.197	4.450	5.418	4.800	5.352
Maximum percentage increase.....		212.9%	228.8%	217.2%	214.7%	235.7%	218.2%

course of water retention as observed in the seeds. The results show the relative differences in the increase until a maximal point is reached, after which the retention of water lessens. An increase in the amount

<sup>2</sup> The final dry weight of the seeds was not determined, and hence the differences in the amount of material acted upon by the solutions are not known in this set of seeds. The data obtained more recently are reserved for a future publication.

of either acid or alkali above these limits retards the reaction, and finally when sufficient acid or alkali is present the catalytic action is completely arrested. There is a constantly increasing diffusion of by-products from the seeds into the solution surrounding them. Accurate measurements of the hydrogen or hydroxyl ion concentration in the reacting mixtures were not attempted in this case. It is clear from these experiments that the variations in the amount of water absorbed and retained must be due to changes which are induced by the solutions within the cells and tissues of the seeds. Briefly stated, the following are the conclusions of importance in this discussion:

1. Seeds of *Phaseolus multiflorus* swell more and retain greater quantities of water in the solution of any acid than in distilled water (table I).

2. The amount of water that seeds absorb and retain in an acid solution is not dependent upon the concentration of the acid, and is not a function of it. A maximum is attained above which a further increase in the concentration of the acid does not lead to a greater retention of water but to a diminishing one. The decrease in weight is due in part to a loss of food constituents of the cells and is consequent upon a series of changes in the cells and tissues through which their physico-chemical state is progressively altered.

3. When equinormal acids are compared the amount of water retained is greater in  $\text{H}_2\text{SO}_4$  than in  $\text{HCl}$  or in  $\text{HNO}_3$ . The two acids first named are about equally dissociated and yield a higher concentration of hydrogen ions than the equinormal  $\text{HNO}_3$ , but the amount of water retention induced seems to be determined not by the concentration so much as by the effect of the anions of the particular acid concerned. The order of the effectiveness of the anions in accelerating the water content is  $\text{SO}_4$ ,  $\text{Cl}$  and  $\text{NO}_3$ .

4. The addition to the solution of  $\text{HCl}$   $n/800$  of any salt not reacting with the acid does not decrease the quantity of water absorbed and retained by seeds of *Phaseolus* (table II). The amount retained is still further increased if  $\text{K}_2\text{SO}_4$  is added. However, a higher concentration of any salt is followed by an inhibition in the capacity for absorbing and retaining water. The effects of molecularly equivalent salt solutions in a solution of  $n/800$  hydrochloric acid are not only unequal in degree but in their time reaction as well. The rate at which the absorbing and retaining power for water develops and passes away in the seeds is most rapid with  $\text{K}_2\text{SO}_4$ . In the series of

TABLE II  
EFFECT OF HCl  $n/800$  SOLUTION WITH VARIOUS EQUIMOLECULAR SALT SOLUTIONS UPON THE WATER CONTENT OF PHASEOLUS SEEDS

Time Interval in Hours			50 c.c. HCl $n/800$ + 50 c.c.									
Hours	Minutes	H <sub>2</sub> O	HCl $n/800$	CaCl <sub>2</sub> $n/800$	NaCl $n/800$	KCl $n/800$	KNO <sub>3</sub> $n/800$	K <sub>2</sub> SO <sub>4</sub> $n/800$	CaH <sub>2</sub> PO <sub>4</sub> $n/800$	C <sub>6</sub> H <sub>5</sub> NO <sub>6</sub> $n/800$	C <sub>2</sub> H <sub>5</sub> NO <sub>2</sub> $n/800$	
2		2.090	2.580	2.450	2.190	2.110	2.520	2.390	2.420	2.540	2.005	
6	30	2.692	2.835	2.480	2.330	2.325	2.640	2.820	2.860	3.430	2.050	
16	30	3.508	3.510	2.750	2.770	3.070	3.510	3.521	3.325	4.260	2.280	
20	30	4.220	4.305	3.900	4.320	4.750	5.215	4.710	5.035	5.270	3.155	
26	30	4.220	4.545	4.192	4.610	4.930	5.450	5.105	5.270	5.320	3.520	
40	30	4.341	5.180	4.778	4.851	5.075	5.655	5.700	5.400	5.500	4.180	
48	30	4.463	5.452	5.330	4.932	5.105	5.780	5.860	5.350	5.570	4.830	
65	30	4.397	5.478	5.415	4.960	5.100	5.805	5.790	5.330	5.542	4.915	
89	30	4.430	5.510	5.480	4.970	5.070	5.835	5.640	5.260	5.480	4.930	
116	30	4.365	5.520	5.000	4.801	4.750	5.850	5.305	4.862	5.435	4.770	
137	30	4.250	5.540	4.850	4.740	4.740	5.520	5.210	4.941	5.425	4.620	
164	30	4.230	5.465	4.850	4.725	4.720	5.480	5.190	4.980	5.421	4.581	
195	30	4.223	5.410	4.750	4.660	4.680	5.450	5.200	5.010	5.178	4.580	
		4.220	5.418	4.790	4.690	4.690	5.440	5.070	5.040	5.470	4.572	
Maximum percentage increase.....		212.9%	214.7%	224.5%	226.8%	241.9%	232.1%	245.1%	212.2%	219.2%	246.5%	

salts having a common anion the order of effectiveness of the kation is K, Na and Ca, the ion most effective in bringing about an increase in the retention of water being placed first. The order of the effectiveness of the anions is  $\text{SO}_4$ , Cl and  $\text{NO}_3$ . This order is nearly identical with that in which the different acids affect the water retaining capacity of seeds.

5. The addition of equimolecular solutions of non-electrolytes to an  $n/800$  HCl solution (table II) does not increase to any extent the amount of water retained by seeds. Sucrose brings about greater depression through its presence than dextrose. The most striking exception to the lack of antagonistic action of non-electrolytes is glyocoll. The amino acid accelerates, apparently, both hydrolytic and certain synthetic reactions. An instance of the catalytic action of amino acids is referred to by Dakin (6).

6. The conclusions for the results on the absorption and retention

TABLE III  
THE WATER CONTENT OF BEAN SEEDS (*Phaseolus multiflorus*) IN EQUINORMAL  
ALKALINE SOLUTIONS  
Two seeds in each 100 c.c. solution

Time Interval in Hours		H <sub>2</sub> O	KOH $n/800$	NH <sub>4</sub> OH $n/800$	Ca(OH) <sub>2</sub> $n/800$	NaOH $n/800$
Hours	Minutes					
		2.090	2.890	2.020	2.051	2.260
2		2.692	2.930	2.550	2.110	2.910
6	30	3.508	3.081	3.650	2.240	3.240
16	30	4.220	3.992	4.255	3.220	3.405
20	30	4.220	4.477	4.300	3.861	3.560
26	30	4.341	5.350	4.380	4.239	4.195
40	30	4.463	6.650	4.480	4.500	4.930
48	30	4.397	6.745	4.500	4.563	4.980
65		4.430	6.725	4.545	4.622	5.060
89	30	4.365	6.650	4.532	4.660	4.950
116		4.250	6.323	4.428	4.690	4.922
137	30	4.230	6.407	4.315	4.700	4.843
164	30	4.223	6.410	4.220	4.692	4.845
195		4.220	6.460	4.151	4.688	4.810
Maximum percentage increase. . . . .		212.9%	233.4%	225.%	224.4%	223.8%

of water by seeds in the alkaline solutions are the analogue of those for the acids (table III). Seeds of *Phaseolus multiflorus* absorb and retain more water in the solution of any alkali than in distilled water. Only within certain limits of concentration is there an increase in the

quantity of water retained, and after this point is exceeded a further increase or decrease in concentration is followed by a diminution in the amount of water held. When equinormal solutions are compared, the amount of water absorbed and retained by seeds is greater in some alkalies than in others. Seeds of *Phaseolus* swell more in KOH than in  $\text{NH}_4\text{OH}$ , and more in either of these than in CaOH or NaOH in the order named. The kations Ca and Na are apparently more active in bringing about a reduction in the water content of cells than either  $\text{NH}_4$  or K,—an order of effectiveness nearly the same as in the results with the molecularly equivalent salt solutions in a solution of HCl.

7. Upon comparison of the amounts of water absorbed and retained in equinormal solutions of acids and alkalies (tables I and III) it is found that seeds of *Phaseolus* swell less and retain much less water in an acid medium than in an alkaline solution.

The course of the absorption and retention of water in corn seeds

TABLE IV  
THE WATER CONTENT OF CORN SEEDS (*Zea mays*) IN ACID SOLUTIONS  
Four seeds in each 100 c.c. solution

Time Interval in Hours		H <sub>2</sub> O	H <sub>2</sub> SO <sub>4</sub> n/800	HNO <sub>3</sub> n/800	HCl n/800	HCl n/3,200	HCl n/6,400
Hours	Minutes						
		1.100	1.050	1.070	1.180	1.050	1.035
2		1.270	1.230	1.300	1.390	1.310	1.211
6	30	1.400	1.340	1.390	1.500	1.390	1.319
16	30	1.540	1.460	1.510	1.620	1.480	1.435
20	30	1.563	1.500	1.540	1.670	1.510	1.460
26	30	1.642	1.565	1.600	1.735	1.550	1.510
40	30	1.715	1.630	1.680	1.805	1.580	1.580
48	30	1.750	1.660	1.700	1.830	1.615	1.610
65		1.800	1.702	1.725	1.880	1.620	1.642
89	30	1.802	1.702	1.750	1.880	1.640	1.675
116		1.800	1.720	1.735	1.905	1.640	1.690
137	30	1.800	1.725	1.726	1.921	1.625	1.690
164	30	1.800	1.750	1.704	1.950	1.630	1.660
195		1.800	1.720	1.700	1.939	1.630	1.658
Maximum percentage increase.....		163.6%	166.6%	164.5%	165.2%	156.2%	163.2%

(*Zea mays*) corroborates many of the various results stated above (tables IV to VI). The seeds show in particular a greater water content in solutions of acids and alkalies than in distilled water; they retain varying amounts of water in equinormal solutions of

different acids and alkalis; there is the analogous lack of relationship between concentration and the capacity for water retention: an optimal point is reached beyond which a further concentration of the acid or alkali is not followed by a greater water content but by a lesser one; the effectiveness of the anion  $\text{SO}_4$  of the particular acid concerned is the same; the increase is greater in alkaline than in equally concentrated acid solutions; the order of the effectiveness of the anions of equimolecular salt solutions in an acid medium (table V) is the same as that observed in the series above; and the action of the non-electrolytes is comparatively similar in this regard.

Important differences, however, exist between the two kinds of seeds which are not without their physiological interest. The amount of water that may be taken up by corn seeds is much smaller than that which can be retained by the seeds of the bush bean. The results for the anions of the equinormal acid and alkaline solutions are more nearly alike than those for the kations. The general grouping of K and Ca for seeds of *Zea mays* (table VI) is the reverse of that observed in *Phaseolus multiflorus*, Ca being more active in bringing about an increase in the water content than K, and this more than Na. The velocity of the reaction is decreased when sodium takes the place of calcium. As the increase in weight between Ca and K in these experiments is considerable, the difference in the reaction must be looked for not in the external conditions of temperature, etc., for they were the same, but in the essential differences of the cell constituents of the two kinds of seeds and their reactions in these solutions.

Another point of interest in this connection is the definite and distinct decrease in the capacity of corn seeds to absorb and retain water with any addition of osmotically equivalent concentrations of certain salts (table V). The anions Cl and  $\text{NO}_3$  are again nearly alike in the degree of their effectiveness in lowering the water content, while the kations Ca and K increase the amount of water retained by the seeds. Sucrose shares with the electrolytes Na and K the marked power of reducing the water retaining capacity of seeds in an acid solution; on the other hand, dextrose and glycocoll produce a definite acceleration, but the former more so than the latter when starches are affected.

These results seem to justify the general conclusion that the variations in the water content of seeds cannot be brought about solely through the concentration of acids or alkalis within the cells and



TABLE V  
EFFECT OF HCl  $n/800$  SOLUTIONS WITH VARIOUS EQUIMOLECULAR SALT SOLUTIONS UPON THE WATER CONTENT OF  
*Zea mays* SEEDS

Four seeds in each 100 c.c. solution

Time Interval in Hours		50 c.c. HCl $n/800$ + 50 c.c.									
Hours	Minutes	H <sub>2</sub> O	HCl $n/800$	CaCl <sub>2</sub> $n/800$	NaCl $n/800$	KCl $n/800$	KNO <sub>3</sub> $n/800$	K <sub>2</sub> SO <sub>4</sub> $n/800$	CaH <sub>24</sub> O <sub>11</sub> $n/800$	CaH <sub>10</sub> O <sub>6</sub> $n/800$	C <sub>6</sub> H <sub>5</sub> NO <sub>2</sub> $n/800$
2		1.100	1.180	1.100	1.060	1.130	1.090	1.060	1.120	1.150	1.120
6	30	1.270	1.390	1.290	1.272	1.380	1.300	1.280	1.330	1.380	1.372
16	30	1.400	1.500	1.385	1.370	1.483	1.380	1.370	1.431	1.485	1.460
20	30	1.540	1.620	1.500	1.480	1.610	1.480	1.500	1.562	1.610	1.580
26	30	1.563	1.670	1.530	1.500	1.630	1.520	1.525	1.590	1.655	1.622
26	30	1.642	1.735	1.610	1.563	1.690	1.585	1.580	1.650	1.735	1.681
40	30	1.715	1.805	1.680	1.600	1.750	1.660	1.630	1.700	1.805	1.755
48	30	1.750	1.830	1.710	1.621	1.750	1.680	1.660	1.720	1.820	1.760
65		1.800	1.880	1.765	1.650	1.780	1.720	1.700	1.772	1.845	1.810
89	30	1.802	1.880	1.850	1.660	1.800	1.733	1.730	1.800	1.890	1.840
116		1.800	1.905	1.875	1.655	1.815	1.740	1.750	1.800	1.880	1.865
137	30	1.800	1.921	1.875	1.670	1.825	1.740	1.765	1.800	1.900	1.870
164	30	1.800	1.950	1.855	1.690	1.810	1.750	1.795	1.800	1.970	1.880
195		1.800	1.939	1.853	1.685	1.818	1.750	1.820	1.800	1.920	1.872
Maximum percentage increase.....		163.6%	165.2%	170.4%	159.4%	161.5%	160.5%	171.6%	160.7%	171.3%	167.8%

tissues. The alterations produced by the variety of substances here used are more easily understood on the hypothesis that hydrolytic cleavages are taking place whereby the water component in the seeds varies the greater in proportion the nearer the equilibrium point reaches to the position of complete hydrolysis. Neither the osmotic pressure of the cell contents is raised to any considerable extent,—for the solutions in which the seeds are kept show increasingly larger amounts of diffusing products of the reaction which in the case of the hydroxides alter the catalyst itself,—nor can any conception of colloidal swelling alone be brought into harmony with the maximal values of water retained, or with the series of chemical changes actually taking place, through which the seeds are progressively altered.

TABLE VI  
THE WATER CONTENT OF CORN SEEDS (*Zea mays*) IN EQUINORMAL ALKALINE SOLUTIONS

Four seeds in each 100 c.c. solution

Time Interval in Hours		H <sub>2</sub> O	KOH <i>n</i> /800	NH <sub>4</sub> OH <i>n</i> /800	Ca(OH) <sub>2</sub> <i>n</i> /800	NaOH <i>n</i> /800
Hours	Minutes					
		1.100	1.130	1.080	1.090	1.010
2		1.270	1.430	1.325	1.315	1.250
6	30	1.400	1.510	1.430	1.400	1.340
16	30	1.540	1.632	1.566	1.525	1.430
20	30	1.563	1.658	1.604	1.560	1.460
26	30	1.642	1.710	1.640	1.620	1.520
40	30	1.715	1.770	1.720	1.711	1.583
48	30	1.750	1.803	1.750	1.726	1.608
65		1.800	1.832	1.812	1.771	1.666
89	30	1.802	1.855	1.860	1.825	1.685
116		1.800	1.870	1.877	1.863	1.680
137	30	1.800	1.830	1.890	1.860	1.710
164	30	1.800	1.830	1.840	1.855	1.710
195		1.800	1.830	1.832	1.845	1.709
Maximum percentage increase.....		163.6%	171.7%	175.%	176.4%	169.3%

There are now at our disposal a few data which may be utilized in the further consideration of the problem of the relation of transpiration to the water content of growing plants. The plants used in the experiments discussed below were tomato cuttings of known green weight and as nearly alike as possible in transpiration surface. The method pursued has been described in previous publications (3). The plants were fastened to perforated stoppers by means of small amounts

of cotton and transferred to sterilized glass bottles of 250 c.c. capacity. Each solution contained one plant and each experiment was continued for 15 to 20 days under greenhouse conditions. A record was made every five days of the weight of water absorbed, the quantity transpired, and the gain or loss in the weight of plants. The curves of figures 1 to 4 are based upon the data contained in tables IX to X, and indicate graphically the course of the water relation. It may be remarked, incidentally, that the physiological reactions of the plants proceed at an unequal pace in the various solutions, even though the external conditions which affect the rate are kept alike. The noteworthy points are that the progress, as represented graphically, attains in almost all cases a maximum on the fifth day; thence the rate falls off rapidly,—with a recoil and nearly proportional lowering on the tenth day; after the adjustment has occurred there is a gradual increase in responsiveness to the solution which becomes more characteristic on the fifteenth day. A moment's study of the data or of a few of the curves will show how hazardous are conclusions concerning the stimulating or inhibiting effect of a solution when based upon results made at arbitrary intervals of time or under unlike conditions. Another point of interest is the fact that during the first five days, stimulation and the rate of the reaction is much more rapidly effected by acid than by the same concentration of alkali (tables VII and VIII). A very striking contrast is obtained also by observing that an increase in size of the root system is not necessarily connected with an accelerating action upon absorption or transpiration (tables IX to XII).

The chief results of the experiments may be described as follows:

1. During a period of fifteen days, tomato cuttings absorb and transpire less water in an acid solution of the concentration here employed than in distilled water (table VII). An exception is  $\text{H}_2\text{SO}_4$   $n/3200$ . The plants absorb more water in a  $\text{HNO}_3$   $n/800$  than in an equinormal  $\text{HCl}$  solution, and less in sulfuric and acetic acids in the order named. There is a great difference in the relationship between the quantity absorbed and transpired and the concentration of the acid. A point is reached in the solution of  $\text{HCl}$  and  $\text{H}_2\text{SO}_4$  beyond which a further increase or decrease in concentration is followed by a diminished absorption and loss of water, while in solutions of  $\text{HNO}_3$  and  $\text{CH}_3\text{COOH}$  the absorption and transpiration of water varies inversely as the concentration.

2. At the concentrations employed the absorption and transpira-

TABLE VII  
WATER RELATION OF TOMATO CUTTINGS IN ACID SOLUTIONS  
Values in grams for 15 days

Solution	Absorbed		Transpired		Retained		Remarks
	5th Day	15th Day	5th Day	15th Day	5th Day	15th Day	
1. $\text{H}_2\text{O}$ .....	8.790	5.920	8.085	5.855	0.705	0.065	Roots 2-5 mm. Plant wilted; immersed por- tion of stem gelatinized; no roots.
2. $\text{HCl}$ $n/800$ .....	6.866	1.830	6.590	1.880	0.276	-0.050	
3. $\text{HCl}$ $n/3,200$ .....	11.720	5.340	10.965	5.230	0.755	0.110	Roots 1-2 mm.
4. $\text{HCl}$ $n/6,400$ .....	9.080	5.010	8.545	4.945	0.535	0.120	Roots 2-5 mm.
5. $\text{H}_2\text{SO}_4$ $n/800$ .....	8.350	1.080	8.230	1.260	0.120	-0.180	Plant wilted; immersed por- tion of stem gelatinized; no roots.
6. $\text{H}_2\text{SO}_4$ $n/3,200$ .....	16.100	6.750	15.260	6.675	0.840	0.075	Roots 1-3 mm.
7. $\text{H}_2\text{SO}_4$ $n/6,400$ .....	10.965	4.060	10.325	4.125	0.640	-0.065	Roots 2-4 mm.
8. $\text{HNO}_3$ $n/800$ .....	12.205	2.030	11.940	2.500	0.265	-1.450	Plant dead. Immersed por- tion of stem gelatinized; no roots.
9. $\text{HNO}_3$ $n/3,200$ .....	11.820	5.090	11.180	5.070	0.640	0.005	Roots 2-3 mm.
10. $\text{HNO}_3$ $n/6,400$ .....	14.105	4.230	13.230	4.260	0.875	0.145	Roots 2-5 mm.
11. $\text{CH}_3\text{COOH}$ $n/800$ ...	5.390	0.960	6.100	1.080	-0.710	-0.120	Plant dead. Immersed por- tion of stem gelatinized. no roots.
12. $\text{CH}_3\text{COOH}$ $n/3,200$ ..	7.515	1.380	7.940	1.310	-0.425	0.070	Plant wilting; no roots.
13. $\text{CH}_3\text{COOH}$ $n/6,400$ ..	11.050	4.390	10.330	4.860	0.720	0.050	Roots 2-9 mm.

Atmometer 49 c.c.-33 c.c.-28 c.c.

Temperature  $8^{\circ}\text{--}35^{\circ}\text{C}$ .

Rel. humidity 38% $\text{--}100\%$ .

Barometer 29.15-29.95 cm.

tion of water by tomato plants in alkaline solutions is less than in distilled water (table VIII). An exception is the KOH  $n/6400$  solution. The alkalies show the following order of effectiveness in which the kation bringing about the least inhibition is placed first: K, Na, Ca,  $\text{NH}_4$ . As in the case of the acids, there is no relationship between increase in concentration of alkali and the increase in the amount of water absorbed and transpired. Beyond a certain optimal point a further increase or decrease in concentration leads to a diminished water relation.

3. If the quantities of water absorbed and transpired in equinormal solutions of acids and alkalies are compared, the serial weighings show that tomato plants function better in an alkaline medium than in one of acid.

In tables VII and VIII are seen also the effects of the solutions upon the amounts of water retained by the plants. In every case the acid inducing the higher absorption and transpiration increased the retention of water. This correspondence is not so marked, however, in the case of the alkaline solutions 5, 7, 12, and 13 (table VIII).

The wilting observed in solutions 2, 5, 8, 11, and 12 (table VII) is the result of transpiration exceeding absorption, while that in solutions 7, 10, and 13 (table VII) and 4 (table VIII) as well as that in 3, 4, 5, 6, 7, 12 and 13 (table IX), 4 (table X) is primarily a loss in food constituents within the plant. Similar facts were mentioned in an earlier paper (5). These few data upon wilting in relation to the different solutions show nearly as many wilting coefficients for plants as there are solutions, atmospheric conditions and energy relations within the plants.

The reduction of the water content to incipient wilting and permanent wilting can be studied more easily in this manner, and the method here used should be of great use in ecological investigations on that account.

4. The addition to a solution of HCl  $n/800$  of any salt in the same molecular concentration inhibits in all cases the action of the acid and increases the amount of water absorbed and transpired. The different salts are unequally effective in this regard. The curves in figures 1 to 4 represent graphically the course of the reaction. In the series of chlorides (table IX) K is more powerful in producing an increase in the water requirement of the plants than Na or Ca. The general grouping of these ions is very similar to that given for the kations in

table VIII on the effects of different alkalies. In the series of sulfates and nitrates, Na is more effective than K or Ca. A comparison of the effectiveness of the anions needs no further comment. The order is  $\text{NO}_3$ ,  $\text{SO}_4$  and Cl, very nearly that of the grouping of anions in the acid solution (table VII). The order of the anions, as that of the kations, is not always readily apparent as an inspection of the serial weighings will show. While in the last five or ten days of the experiment the order is as given above, it may appear inversely in the earlier part of the experiment. The changes are undoubtedly due to the removal of food constituents and to alterations in the contents of cells.

The marked effect of glycocoll among the non-electrolytes in counteracting the action of hydrochloric acid is not shared by dextrose or sucrose. The latter has the least effect of any of the various salts added upon the quantity of water absorbed and transpired by tomato plants.

5. The presence of any salt in equimolecular concentration in the solution of an alkali does not in all cases increase the amount of water absorbed and transpired by tomato plants. In table X the difference in the quantities of the water relation induced through the action of electrolytes and non-electrolytes of the same concentration, it is easily noted, is not as great as in an acid solution.

The effect of any salt seems to be made up of the sum of the effects of the constituent ions. The kations arrange themselves in about the following order in which the most effective in increasing the water supply is placed first in the series: Ca, Na, K. The relation in the order of the anions is not readily apparent, but it is of interest to note that in an alkaline solution the nitrate of calcium brings about a greater reduction in the available water for transpiration and absorption than the nitrate of potassium.

If the amounts are compared which the plants absorb and transpire in acid and alkaline solutions through the action of equimolecular solutions of salts added to them, it will be seen that the plants function more evenly in an alkaline medium.

Non-electrolytes, through their presence in osmotically equivalent concentrations, reduce the water relation of tomato plants in an alkaline medium, but not to the extent as in an acid solution. Comparison readily shows that the amount of the difference is considerably above that in distilled water or in  $\text{HCl } n/800$ .

TABLE VIII  
WATER RELATION OF TOMATO CUTTINGS IN ALKALINE SOLUTIONS  
Values in grams for 15 days

Solution	Absorbed			Transpired			Retained		Remarks
	5th Day	10th Day	15th Day	5th Day	10th Day	15th Day	5th Day	10th Day	
1. $H_2O$ .....	8.790	5.920	8.600	8.085	5.855	8.390	0.705	0.065	Roots 2-5 mm.
2. KOH $n/800$ .....	6.910	7.390	8.840	6.560	7.280	8.530	0.350	0.210	Roots 3-12 mm.
3. KOH $n/3,200$ .....	4.225	3.900	6.310	3.990	3.770	6.100	0.235	0.130	Roots 8-20 mm.
4. KOH $n/6,400$ .....	15.240	7.980	13.780	14.500	8.760	12.550	0.740	-0.780	Roots 3-16 mm.
5. $NH_4OH$ $n/800$ .....	4.835	4.870	5.470	4.450	4.760	5.210	0.385	0.110	Roots 2-3 mm.
6. $NH_4OH$ $n/3,200$ .....	5.550	5.580	8.390	5.070	5.400	8.190	0.480	0.200	Roots 3-8 mm.
7. $NH_4OH$ $n/6,400$ .....	4.430	3.770	6.790	4.065	3.660	6.520	0.365	0.110	Roots 3-5 mm.
8. $Ca(OH)_2$ $n/800$ .....	5.670	7.640	8.660	5.300	7.390	8.370	0.370	0.250	Roots 10-55 mm.
9. $Ca(OH)_2$ $n/3,200$ .....	3.460	6.415	9.790	3.130	6.250	9.500	0.330	0.165	Roots 10-22 mm.
10. $Ca(OH)_2$ $n/6,400$ .....	7.310	4.690	7.070	7.010	4.620	6.800	0.300	0.070	Roots 3-12 mm.
11. NaOH $n/800$ .....	4.460	7.060	10.630	4.015	6.840	10.270	0.445	0.220	Roots 10-23 mm.
12. NaOH $n/3,200$ .....	2.870	5.015	4.525	2.530	4.880	4.420	0.340	0.135	Roots 3-5 mm.
13. NaOH $n/6,400$ .....	7.840	4.635	6.215	7.110	4.580	6.120	0.370	0.055	Roots 3-5 mm.

Atmospheric conditions as in table VII.

TABLE IX

WATER RELATION OF TOMATO CUTTINGS IN HCl  $n/800$  WITH VARIOUS EQUIMOLECULAR SALT SOLUTIONS

Values in grams for 20 days in 5-day periods

Solution	Quantity of Water			Remarks
	Absorbed	Transpired	Retained	
1. H <sub>2</sub> O .....	5.350 4.120 9.520 13.260	4.960 3.790 9.260 12.670	0.390 0.330 0.260 0.590	Roots 12-15 mm.
2. HCl $n/800$ .....	5.040 1.170 0.830 1.560	5.150 1.030 1.010 2.290	-0.110 0.140 -0.180 -0.730	
3. HCl $n/800$ + KCl $n/800$ .	12.050 4.480 4.150 3.420	11.525 4.305 4.130 3.620	0.525 0.175 0.020 -0.200	Immersed portion of stem partly gelatinized; few short roots 2-3 mm.
4. HCl $n/800$ + NaCl $n/800$	7.750 2.150 4.860 6.890	7.250 1.930 4.990 6.910	0.500 0.220 -0.130 -0.020	
5. HCl $n/800$ + CaCl <sub>2</sub> $n/800$	8.330 2.960 4.440 4.920	7.900 2.550 4.580 4.920	0.430 0.410 -0.140 0.000	Same as No. 4.
6. HCl $n/800$ + K <sub>2</sub> SO <sub>4</sub> $n/800$	9.810 4.220 4.820 5.090	9.410 3.970 4.840 5.140	0.400 0.250 -0.020 -0.050	
7. HCl $n/800$ + Na <sub>2</sub> SO <sub>4</sub> $n/800$	13.610 4.030 4.780 5.110	12.935 3.805 4.790 5.170	0.675 0.225 -0.010 -0.060	Immersed portion of stem brownish; few short roots 1-3 mm.
8. HCl $n/800$ + CaSO <sub>4</sub> $n/800$	9.650 2.660 6.210 10.180	9.320 2.445 6.070 9.990	0.330 0.215 0.140 0.190	
9. HCl $n/800$ + KNO <sub>3</sub> $n/800$	9.470 3.790 6.515 9.755	9.050 3.460 6.320 9.360	0.420 0.330 0.195 0.395	As above; few short roots 1-4 mm.
10. HCl $n/800$ + NaNO <sub>3</sub> $n/800$	19.900 6.840 8.580 9.755	19.150 6.540 8.220 9.360	0.750 0.300 0.360 0.395	



TABLE IX—*Continued*

Solution	Quantity of Water			Remarks
	Absorbed	Transpired	Retained	
11. HCl <i>n</i> /800+	9.190	8.810	0.380	As above in No. 10; roots 1-3 mm.
	4.770	4.460	0.310	
CaNO <sub>3</sub> <i>n</i> /800	8.600	8.310	0.290	
	12.710	12.270	0.440	
12. HCl <i>n</i> /800+	9.230	8.920	0.310	Immersed portion of stem gelatinized; roots 1-2 mm.
	2.070	1.980	0.090	
C <sub>12</sub> H <sub>22</sub> O <sub>11</sub> <i>n</i> /800	2.250	2.370	-0.120	
	1.460	1.680	-0.220	
13. HCl <i>n</i> /800+	8.630	8.300	0.330	Immersed portion of stem gelatinized; brownish; few short roots 1-3 mm.
	3.350	3.190	0.160	
C <sub>6</sub> H <sub>12</sub> O <sub>6</sub> <i>n</i> /800	4.390	4.190	0.200	
	5.160	5.280	-0.120	
14. HCl <i>n</i> /800+	13.800	13.280	0.520	As above in No. 13; roots 1-6 mm.
	5.380	5.110	0.270	
C <sub>2</sub> H <sub>5</sub> NO <sub>2</sub> <i>n</i> /800	8.830	8.450	0.380	
	12.470	12.080	0.390	

6. The effects of the reaction of solutions on the quantity of water retained by the plants and on the green weight of roots and tops are most markedly shown in tables XI and XII. In every case where salts have been added to HCl *n*/800, the amount of water retained and the actual gain in the weight of the plants is greater than that in the corresponding hydrochloric acid solution without salts. Especially is this the case where glycocoll and the nitrates of Na, Ca and K had been used. The chlorides are more effective than the sulfates in bringing about a reduction in the amount of water that the plants can retain. The figures also show that the least increase is found in the sucrose solution.

The table (XI), moreover, brings out some interesting data on the changes in the metabolism of the plants. The difference between the actual gain of the plants—*i. e.*, the increase in weight above the initial green weight—and the total amount of water retained, is greater in the nitrates of Na and Ca than in their sulfates or chlorides.

This order of the effectiveness of the anions, it will be noted, is reversed with the salts of K; the acceleration is in the order Cl, SO<sub>4</sub>, NO<sub>3</sub>. There is no difficulty in discovering that equimolecular concentrations of glycocoll and sodium nitrate when added to HCl *n*/800 are nearly alike in their efficiency to increase the constructive processes in general, and that NaCl and sucrose induce the greatest

depression in the developmental reactions. In the one case both the release of energy and the accumulation of food material are stimulated in the presence of these salts, while in the other case metabolic reactions and the process of translocation of food constituents are considerably retarded. No relationship to transpiration is apparent. Where the selective action of the salts favors metabolism and growth and the leaf surface increases, transpiration is consequently greater also. The relationship, however, is only approximately so. The absorption of water and the absorption of salts are not identical processes (4).

7. In table XII are shown in a similar way the comparative effects of the presence of equimolecular concentrations of salts in an alkaline solution. In almost all cases, the amount of water retained and the actual gain in the green weight of plants is larger than that in distilled water. But when compared with the corresponding solution of KOH  $n/800$  lacking any one of these salts the great difference in the amounts induced through the action of electrolytes and non-electrolytes is readily noted. It is apparent that at the same concentration of alkali the sulfate of calcium is more effective in increasing the water content of the plants than the sulfate of sodium. The order in which the anions are grouping themselves is not as readily made out as in the case of the acid solutions. The causes for these changes, here as in several of the examples cited above, are undoubtedly several in kind, and largely due to the chemical changes taking place within the cells and tissues of the plants. There is no difficulty in recognizing the following order in which the kations are effective, that one producing the greatest reaction being given first: Ca, Na; the position of K is somewhat variable. Again no relationship to the amount of water transpired is noticeable; the selective activity of the salts and their beneficial or injurious effect is independent of the solute. This lack of relationship is most marked upon comparison with the non-electrolytes, and upon observing the reaction of the various salt solutions on the metabolism of the plants. The greatest difference between the quantity of water retained and the actual gain in the green weight of the plants is obtained in  $\text{CaCl}_2$ ; the least difference is found in KCl. Of extreme importance in this connection is the gain in the weight of plants over and above the amount of water retained by them in the alkaline solutions of glycocoll and sucrose. There seems scarcely any doubt that the organic compounds accelerate both the hydrolytic and the synthetic reactions.

TABLE X

WATER RELATION OF TOMATO CUTTINGS IN KOH  $n/800$  WITH VARIOUS EQUIMOLECULAR SALT SOLUTIONS

Values in grams for 20 days in 5-day periods

Solution	Quantity of Water			Remarks
	Absorbed	Transpired	Retained	
1. $H_2O$ . . . . .	5.350 4.120 9.520 13.260	4.960 3.790 9.260 12.670	0.390 0.330 0.260 0.590	Roots 12-15 mm.
2. KOH $n/800$ . . . . .	12.660 5.980 15.170 22.320	12.290 5.515 14.440 21.595	0.370 0.465 0.730 0.725	Roots 15-30 mm.
3. KOH $n/800$ + KCl $n/800$	6.420 3.410 8.075 14.405	6.200 3.020 7.870 13.875	0.220 0.390 0.205 0.530	Roots 5-11.5 mm.
4. KOH $n/800$ + NaCl $n/800$	10.980 6.670 20.185 28.875	9.615 7.025 19.165 28.195	1.365 -0.355 1.020 0.680	Roots 20-50 mm.
5. KOH $n/800$ + CaCl <sub>2</sub> $n/800$	12.720 6.810 19.690 28.480	13.270 6.250 18.535 27.685	0.450 0.560 1.155 0.795	Roots 20-35 mm.
6. KOH $n/800$ + K <sub>2</sub> SO <sub>4</sub> $n/800$	7.640 4.470 12.490 20.090	7.350 4.050 12.090 19.560	0.290 0.420 0.400 0.530	Roots 20-40 mm.
7. KOH $n/800$ + Na <sub>2</sub> SO <sub>4</sub> $n/800$	5.555 4.125 11.250 19.100	5.065 3.975 10.820 18.620	0.490 0.150 0.430 0.480	Roots 15-30 mm.
8. KOH $n/800$ + CaSO <sub>4</sub> $n/800$	11.560 8.990 25.870 33.760	11.110 8.030 24.745 32.690	0.450 0.960 1.125 1.070	Roots 20-65 mm.
9. KOH $n/800$ + KNO <sub>3</sub> $n/800$	9.390 4.870 11.300 19.410	8.930 4.420 10.720 18.675	0.460 0.450 0.580 0.735	Roots 20-25 mm.
10. KOH $n/800$ + NaNO <sub>3</sub> $n/800$	8.810 4.895 15.475 29.450	8.465 4.425 14.765 28.850	0.345 0.470 0.710 0.600	Roots 20-35 mm.

TABLE X—*Continued*

Solution	Quantity of Water			Remarks
	Absorbed	Transpired	Retained	
11. KOH <i>n</i> /800 + CaNO <sub>3</sub> <i>n</i> /800	5.000 4.010 20.180 36.980	4.760 2.850 19.660 36.000	0.240 1.160 0.520 0.980	Roots 20–40 mm.
12. KOH <i>n</i> /800 + C <sub>12</sub> H <sub>22</sub> O <sub>11</sub> <i>n</i> /800	5.840 4.780 8.990 17.660	5.280 4.030 8.800 16.930	0.560 0.750 0.190 0.730	
13. KOH <i>n</i> /800 + C <sub>6</sub> H <sub>12</sub> O <sub>6</sub> <i>n</i> /800	4.080 6.940 16.390 26.440	3.830 6.170 15.770 25.750	0.250 0.770 0.620 0.690	
14. KOH <i>n</i> /800 + C <sub>2</sub> H <sub>6</sub> NO <sub>2</sub> <i>n</i> /800	6.630 5.760 18.330 31.640	6.380 5.120 17.485 30.575	0.250 0.640 0.845 1.065	

A comparison regarding the qualitative as well as the quantitative differences between the effects of acids and those of alkalis indicates that in an alkaline medium the metabolic processes and the translocation of food materials go on more readily than under the influence of an acid medium and that the presence of a salt in the one solution gives rise to reactions unlike that in the other medium.

Tentatively the following summary is here presented, the ecological and agricultural significance of which will be evident from the discussion of the results:

1. Different acids and alkalis are unequal in their effectiveness to modify the water relation of plants. At one concentration the influence may be related to the chemical characteristics of the solute concerned, at another concentration it may involve the physico-chemical properties of the solution. The velocity of the action is independent of the concentration of the solution; it increases to a maximum and with further concentration not only inhibits biochemical processes but destroys them. As to the physiological effects of the solutions the order in which acids and alkalis induce absorption and transpiration of water is often different from the order in which the water content or the metabolism of the plants is altered.

2. The effect of adding equimolecular salt solutions of different

kinds to an acid or an alkaline solution shows that the reactions are specific and unlike with each salt employed (pages 421, 423). The order of effectiveness in inhibiting or in producing an increase in the water relations of plants may be stated as follows:

(a) In a solution of hydrochloric acid the salts of sodium counteract to a marked degree the injurious effects of the acid and are preferable to potassium salts. The nitrates of any of these three bases give uniformly better results than the sulfates or chlorides.

Calcium has a greater accelerating action in an unbalanced acid solution if combined with a sulfate, while potassium proves most corrective if used as a chloride. The beneficial effects obtained may be due to an indirect reaction between the different substances in the medium through changes induced by the plant. The acid radicle ( $\text{NO}_3$ ) is usually absorbed more rapidly, leaving behind the base ion or alkaline radicle ( $\text{Na}$ ), which then may give rise to a direct reaction between the different substances in the medium.

(b) In an alkaline medium ( $\text{KOH}$ ) calcium salts are more beneficial and should be furnished preferably in the form of a sulfate. Sodium salts are more capable of altering the water relation of plants as chlorides, and potassium salts give uniformly a greater increase as nitrates. The relative effects of the anions and kations may be accounted for in a manner as pointed out in (a).

3. The remarkable increase in weight which has attended the use of non-electrolytes, especially glycoll and sucrose, proves ready digestibility of these organic compounds, their relative value in the maintenance and repair of constituents destroyed during growth in acid and alkaline solutions, and further indicates that water retention during growth may be limited by any factor which prevents the construction of food constituents, *i. e.* the chemosynthesis of proteins and carbohydrates. If this interpretation is correct, it follows that artificial organic fertilizers may supplement advantageously the use of mineral salts.

4. The injurious properties of acid solutions (and probably also of acid soils and subsoils) may not necessarily be due to their acid character. In itself acidity is not always a disturbing factor to growth and transpiration of plants. The apparent inhibiting action may be the effect of the presence of some salt, perhaps in large measure the reaction of the solutions after the plants have been growing in them for some time, retarding the rate of hydrolysis of substances in the cells of plants.

TABLE XI

TRANSPIRATION AND GROWTH OF TOMATO CUTTINGS IN HCl  $n/800$  WITH VARIOUS  
EQUIMOLECULAR SALT SOLUTIONS

Values in grams for 20 days

Solution	Quantity of Water			Gain or Loss in Weight of Plants	Extent of Chemical Changes within Tissues	Weight of Roots
	Ab- sorbed	Trans- pired	Retained			
1. H <sub>2</sub> O.....	32.250	30.680	1.570	1.140	-0.430	0.185
2. HCl $n/800$ .....	8.600	9.480	-0.880	-1.040	-0.160	0.000
3. HCl $n/800$ + KCl $n/800$ .....	24.100	23.580	0.520	0.190	-0.330	0.010
4. HCl $n/800$ + NaCl $n/800$ .....	21.650	21.080	0.570	0.450	-0.120	0.014
5. HCl $n/800$ + CaCl <sub>2</sub> $n/800$ .....	20.650	19.950	0.700	0.490	-0.210	0.018
6. HCl $n/800$ + K <sub>2</sub> SO <sub>4</sub> $n/800$ .....	23.940	23.360	0.580	0.315	-0.265	0.019
7. HCl $n/800$ + Na <sub>2</sub> SO <sub>4</sub> $n/800$ .....	27.530	26.700	0.830	0.500	-0.320	0.010
8. HCl $n/800$ + CaSO <sub>4</sub> $n/800$ .....	28.700	27.825	0.875	0.630	-0.245	0.020
9. HCl $n/800$ + KNO <sub>3</sub> $n/800$ .....	28.530	28.290	1.340	1.105	-0.235	0.020
10. HCl $n/800$ + NaNO <sub>3</sub> $n/800$ .....	45.075	43.270	1.805	1.350	-0.455	0.018
11. HCl $n/800$ + CaNO <sub>3</sub> $n/800$ .....	35.270	33.850	1.420	1.100	-0.320	0.028
12. HCl $n/800$ + C <sub>12</sub> H <sub>22</sub> O <sub>11</sub> $n/800$ .....	15.010	14.950	0.060	-0.305	-0.245	0.010
13. HCl $n/800$ + C <sub>6</sub> H <sub>12</sub> O <sub>6</sub> $n/800$ .....	21.530	20.960	0.570	0.360	-0.210	0.015
14. HCl $n/800$ + C <sub>2</sub> H <sub>5</sub> NO <sub>2</sub> $n/800$ .....	40.480	38.820	1.660	1.345	-0.315	0.200

5. A further fact of interest from a study of the physiological reactions of the different solutions toward plants here employed and growing under the same group of external conditions is the observation that conceptions of colloidal swelling or a differential osmotic pressure in cells and tissues are in themselves inadequate to account for the varying amounts of water retained by plants, and can not be considered the fundamental factors in absorption. The values of the quantity of water retained do not increase progressively with every increase in the concentration of acid or alkali in the solution surrounding the plants. This leads to the conclusion that the influence of acids and alkalies may be accounted for on the basis of their hydrolyzing power upon the various colloidal and other constituents within the cells. The diffusion of food constituents of seeds out of the cells into the solution surrounding them does not permit an interpretation of the variability in their water content on the basis of differences in osmotic pressure, or from the point of view of that series of physico-chemical phenomena designated as colloidal. Both are unquestionably involved and of importance in the general problem of the water content of plants, but they may well represent only a phase of that greater series of phenomena which is included under the term of hydrolytic reactions.

It is fairly well known that the final equilibrium is not the same in the case of enzyme action as with acids or bases. During the catalytic reactions a number of intermediate compounds arise. The hydrolytic processes are carried farther by acids than by enzymes, and they bring about the greatest changes in materials and in energy transformations, probably owing to diffusion of the products of the reaction. The effects of alkalies are variable, due in large measure to the alteration of the catalyst itself by the reaction, *i. e.*, through the combined effect of neutralization and the production of salts with the

TABLE XII

TRANSPIRATION AND GROWTH OF TOMATO CUTTINGS IN KOH *n*/800 WITH VARIOUS  
EQUIMOLECULAR SALT SOLUTIONS

Values in grams for 20 days

Solution	Quantity of Water			Gain or Loss in Weight of Plants	Extent of Chemical Changes within Tissues	Weight of Roots
	Ab- sorbed	Trans- pired	Retained			
1. H <sub>2</sub> O . . . . .	32.250	30.680	1.570	1.140	-0.430	0.185
2. KOH <i>n</i> /800 . . . . .	56.130	53.840	2.290	1.950	-0.340	0.410
3. KOH <i>n</i> /800 + KCl <i>n</i> /800 . . . . .	32.310	30.965	1.345	1.220	-0.125	0.160
4. KOH <i>n</i> /800 + NaCl <i>n</i> /800 . . . . .	66.710	64.000	2.710	2.520	-0.190	0.480
5. KOH <i>n</i> /800 + CaCl <sub>2</sub> <i>n</i> /800 . . . . .	67.700	64.740	2.960	2.175	-0.785	0.440
6. KOH <i>n</i> /800 + K <sub>2</sub> SO <sub>4</sub> <i>n</i> /800 . . . . .	44.690	33.050	1.640	1.420	-0.220	0.310
7. KOH <i>n</i> /800 + Na <sub>2</sub> SO <sub>4</sub> <i>n</i> /800 . . . . .	40.030	38.480	1.550	1.390	-0.260	0.250
8. KOH <i>n</i> /800 + CaSO <sub>4</sub> <i>n</i> /800 . . . . .	80.180	76.575	3.595	3.265	-0.330	0.830
9. KOH <i>n</i> /800 + KNO <sub>3</sub> <i>n</i> /800 . . . . .	44.970	42.745	2.225	1.750	-0.475	0.260
10. KOH <i>n</i> /800 + NaNO <sub>3</sub> <i>n</i> /800 . . . . .	58.630	56.505	2.125	1.850	-0.275	0.300
11. KOH <i>n</i> /800 + CaNO <sub>3</sub> <i>n</i> /800 . . . . .	66.170	63.270	2.900	2.640	-0.280	0.460
12. KOH <i>n</i> /800 + C <sub>12</sub> H <sub>22</sub> O <sub>11</sub> <i>n</i> /800 . . . . .	37.270	25.040	1.230	1.815	+0.585	0.530
13. KOH <i>n</i> /800 + C <sub>6</sub> H <sub>12</sub> O <sub>6</sub> <i>n</i> /800 . . . . .	53.850	51.520	2.330	2.030	-0.300	0.510
14. KOH <i>n</i> /800 + C <sub>2</sub> H <sub>5</sub> NO <sub>2</sub> <i>n</i> /800 . . . . .	62.360	59.560	1.800	2.775	+0.975	0.700

by-products of the reaction. Hydrolytic and synthetic reactions induce the conditions which favor the retention of water and underlie irregularities in growth as well as the maintenance of a constant weight over long periods of time.

Water not retained in this manner is usually allowed to escape as transpirational water loss. The simple fact that the quantity absorbed is equivalent under certain conditions to the amount transpired does not indicate that the mere consumption of water leads to growth. The growth of plants and their distribution depends in large part upon the amount of water retained within the plants, but the degree of the water-holding capacity (*e. g.*, xerophytism in plants and the suc-

culence of certain species) is not a function of mere water consumption, *i. e.*, of the rate of supply of water to loss by transpiration; nor can it be determined solely from a morphological examination of the structure of the shoot of plants. Transpiration is not primarily the cause of growth. The two are frequently associated and may at times lie so closely together that they give the impression of running parallel with each other in a causal relation. In such cases transpirational values are the consequence of growth *e. g.* in leaf surface. The processes of the absorption of water and that of dissolved substances are not identical but independent of each other.

Another line of evidence in proof of the conception of the chemical changes induced through acids and alkalies and thus reducing or increasing the quantity of retained water, is apparent from a comparison of the differences in the loss of tissue substances or the increase of it by plants under these conditions. The degree of the conversion of colloidal and other cell constituents is paralleled by a change in their affinity for water which is retained from any available source.

The water content of the plants is essentially dependent not only upon the catalytic action of an optimal concentration of acid or alkali but also upon the chemical character of the body material affected. The changes that occur in the cells and tissues may be still further retarded or hastened through the addition of salts.

The results of the experiments described in the foregoing pages show that the reactions obtained from the addition of salts to toxic acid or alkaline solutions may aid in developing further the conception of antagonistic relations among salts. It is not proposed to discuss the views which have been suggested from time to time in regard to the causes of this phenomenon or the manner in which salts correct injurious effects. The effects may be due in part to depression of ionization (11), or to the formation of undissociated salts (2). The valence of ions (12) or their lowered rate of absorption (19) and adsorption (16) may determine the action, and it may be referred to complicated changes in the permeability of the plasmatic membrane of the cells of plants (13, 15), or to the effect of the salts upon protein compounds (9, 10, 20, 21, 14). The results here reported make it probable, and the conclusion seems unavoidable, that no one of the various hypotheses advanced seems to consider the quantitative changes taking place in the material and the energy system within the cells, whereby the contents become altered in their water retaining



capacity through catalytic reactions which accelerate or retard the rate of the hydrolysis of substances in the cells.

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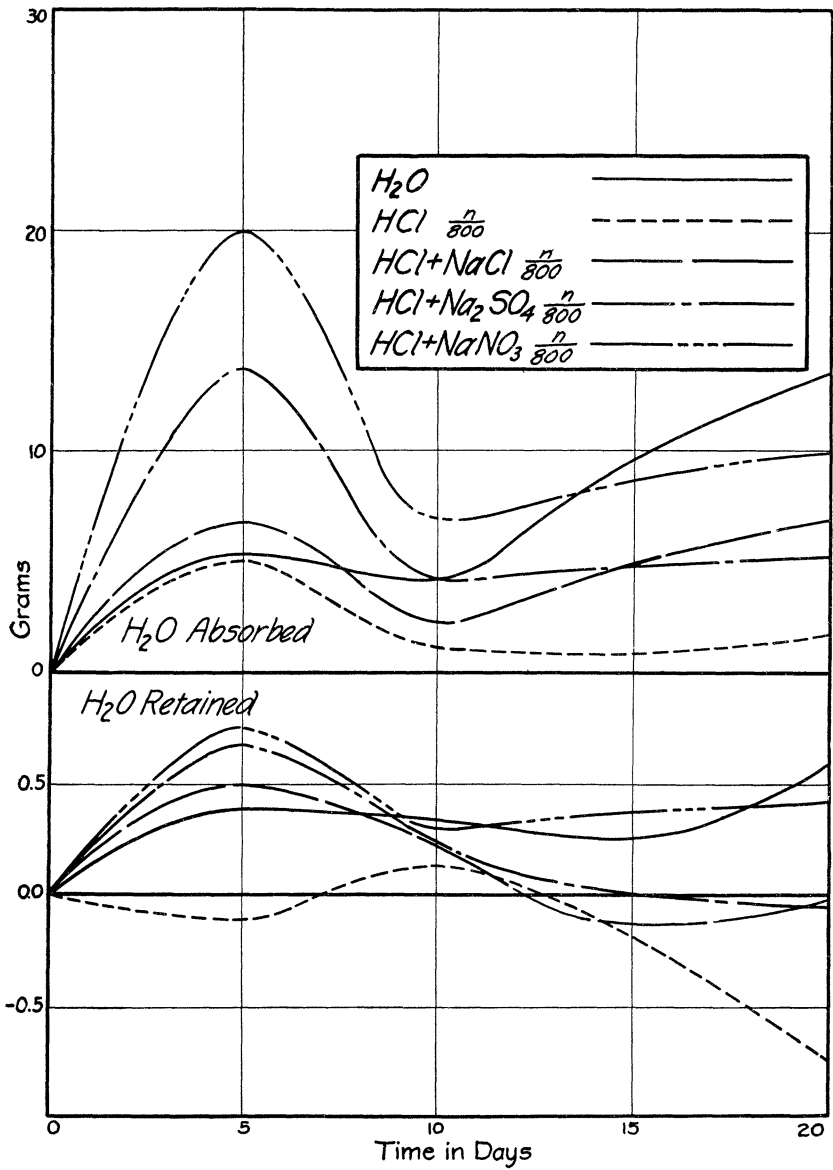


FIG. 1. The effectiveness of anions in a toxic acid solution, (table IX).

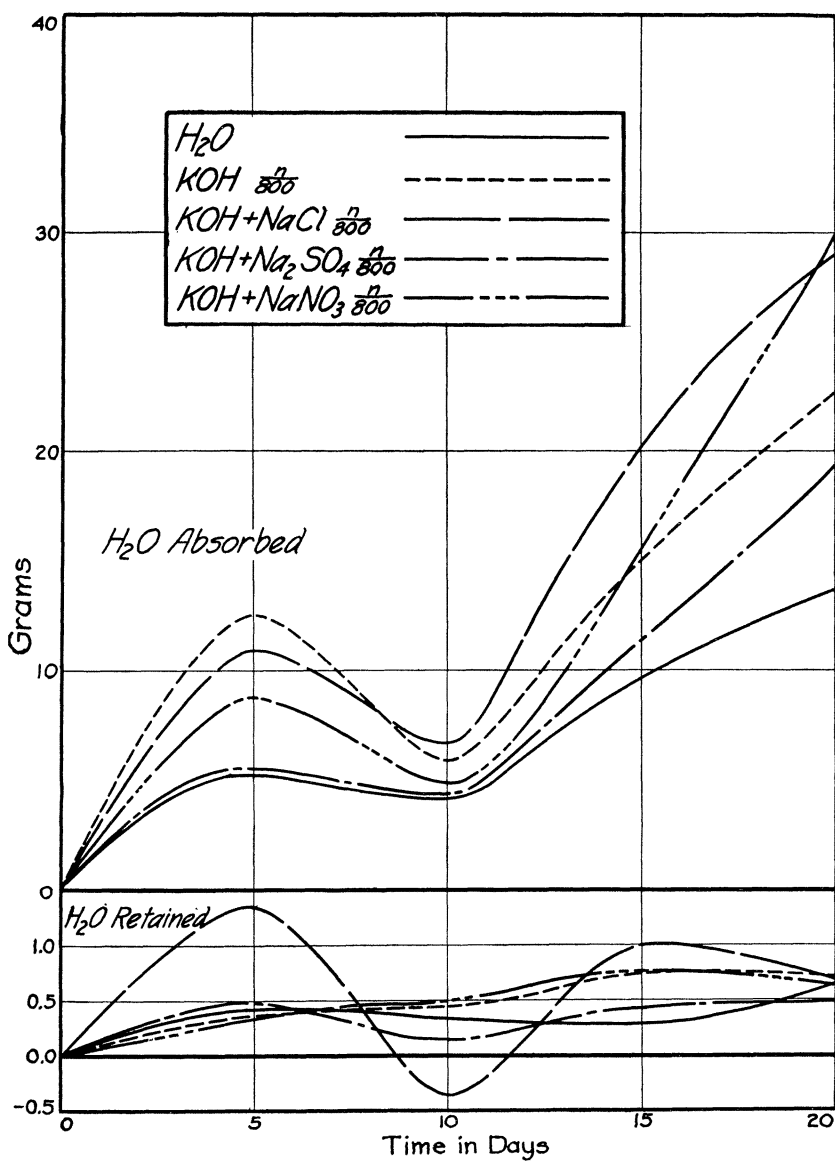


FIG. 2. The effectiveness of anions in a toxic alkaline solution, (table X).

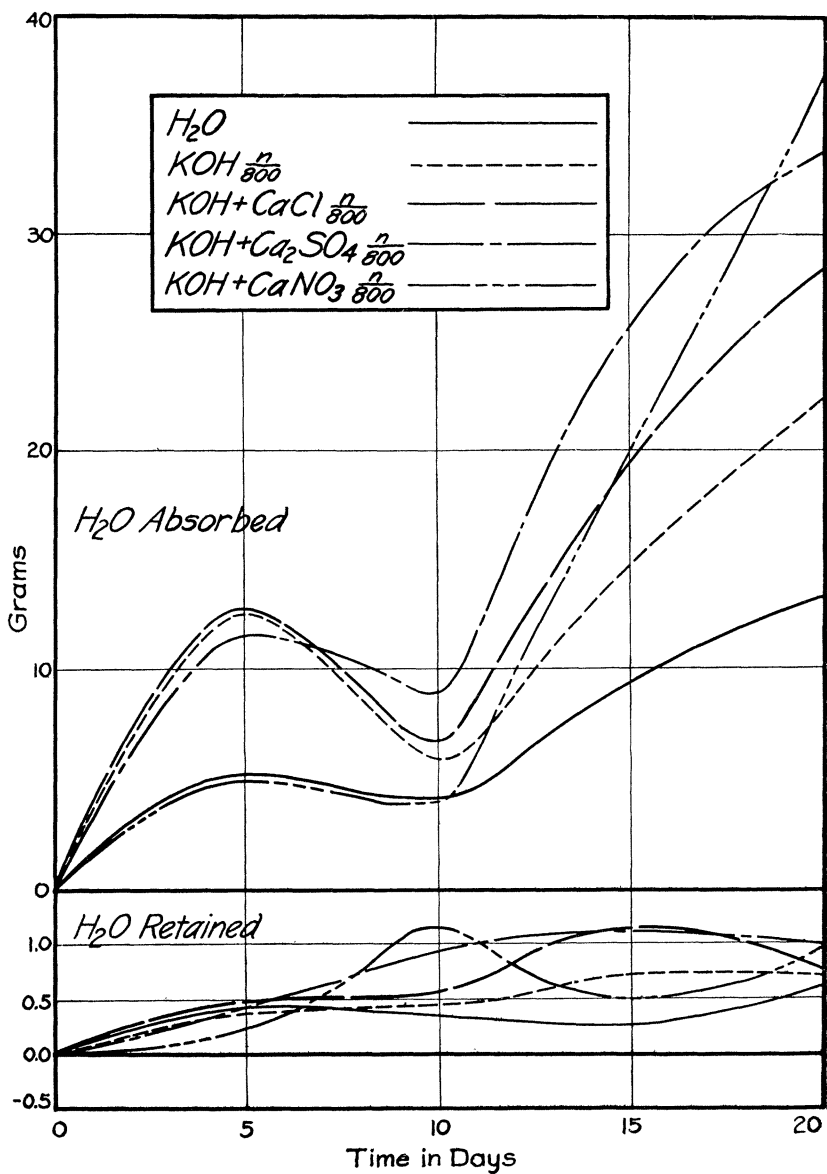


FIG. 3. The effectiveness of anions in a toxic alkaline solution, (table X).

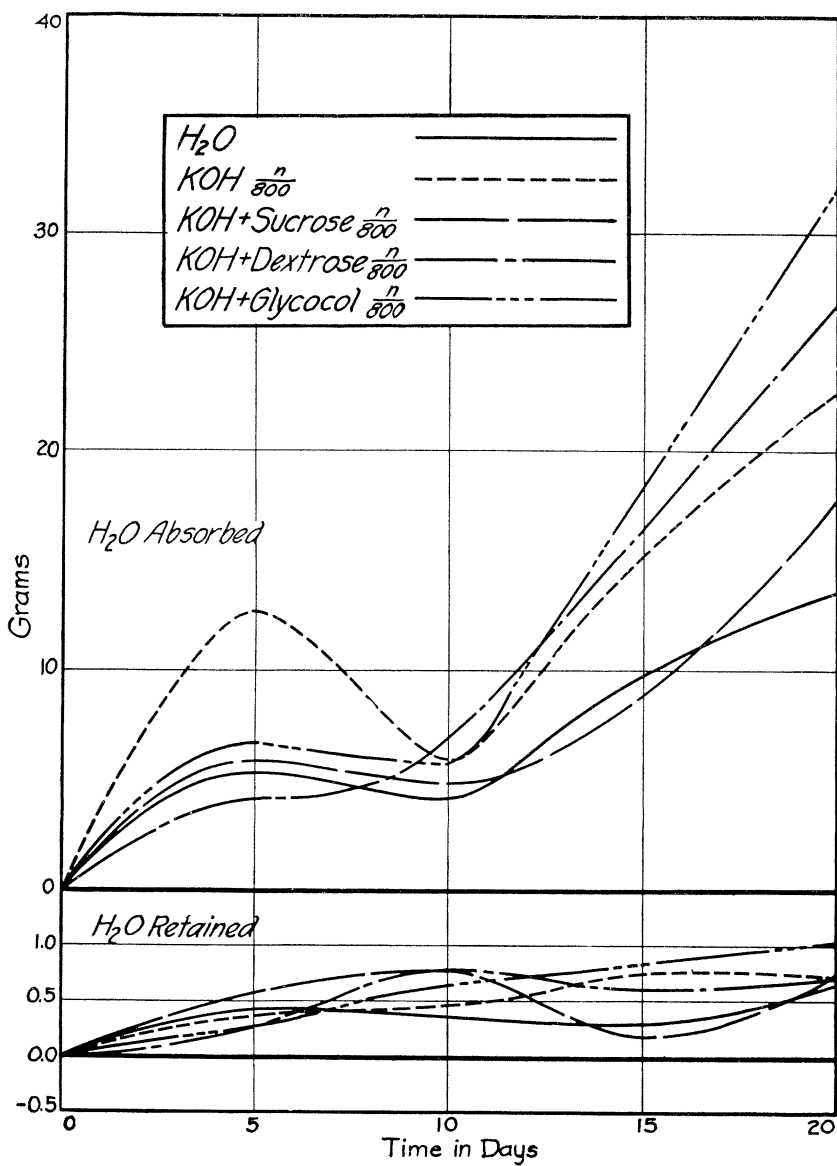


FIG. 4. The effectiveness of non-electrolytes in a toxic alkaline solution, (table X).